THE ACANTHODIAN FAUNA OF THE CRAVEN PEAKS BEDS (EARLY TO MIDDLE DEVONIAN), WESTERN QUEENSLAND

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Two aeanthodian faunas of different ages have been identified from calcareous lithologies assigned to the Cravens Peak Beds, Georgina Basin, western Queensland. A sparse fauna comprising scales of *Nostolepis* sp. cf. *N. striata* and *Radioporacanthodes* sp. indicates a Lochkovian or Pragian age for one shot-hole sample south of the Toko Range. A limestone outcrop further south in the Toomba Range yielded a more abundant fauna which includes dissociated remains of two new acanthodians *Teneracanthus toombaensis* gen. et sp. nov. and *Machaeracanthus pectinatus* sp. nov. *Teneracanthus* gen. nov. is an acanthodid acanthodian which is most similar to the early Frasnian *Lodeacanthus* from Latvia. *M. pectinatus* sp. nov. is based on isolated scales. Comparison with acanthodian and thelodontid microremains from well-dated sequences in the Broken River Group indicate a late Emsian to early Eifelian age for the limestone stratum. □ *Acanthodian, Mesacanthidae, Teneracanthus gen. nov., Machaeracanthidae fam. nov., Machaeracanthus, Cravens Peak Beds, Georgina Basin, Devonian.*

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Devonian fish remains have been known from the Amadeus and Georgina Basins of central Australia for nearly 50 years (Hills, 1959; Gilbert-Tomlinson, 1968; Young, 1985, 1988). Central Australian Devonian rocks are predominantly sandstones and siltstones which, in the absence of marine invertebrate fossils, have been interpreted as fluvial, lacustrine, or aeolian deposits that were laid down at the initial emergence of the central Australian landmass from the ocean. The only known exception is a small limestone outcrop, previously assigned to the basal calcareous unit of the Cravens Peak Beds in the Georgina Basin of western Queensland. This limestone was first sampled for microfossils to confirm its assumed Early Ordovician age, but instead was found to contain an assemblage of Devonian fish remains (Draper, 1976). Various scales of thelodont agnathans and aeanthodians, associated with eridostracans and ostracods, were described by Turner et al. (1981) from this limestone, and from five other (seismic shot-point) localities in the Toko Range area, about 40 km to the north (Fig. 1). They assigned the fauna a probable Emsian age, and associated eridostracans and ostracods were used to infer a probable shallow marine environment of deposition. On this evidence, an elongate marine incursion from the south was included on the palaeogeographic map for the Emsian-Eifelian timeslice of the Devonian by Struckmeyer & Totterdell (1990: 34).

Further collecting (GCY, 1977) revealed exceptionally well preserved but extremely fragile vertebrate remains, which could be extracted by acetic acid digestion. Based on this additional material, Young (1984) described some pterichthyodid antiarch placoderm bones, at the time considered to be one of the oldest records of this group. Turner & Young (1987) described enigmatic chondrichthyan teeth of the shark *Mcmurdodus whitei*, which display advanced features and are comparable to those of the living hexanchid sharks. *Mcmurdodus* was erected by White (1968) for a tooth from the Aztec Siltstone of Victoria Land, Antarctica, which was compared with teeth of the hexanchid *Notidanus*. The fossil record of hexanchids otherwise extends back only to the Jurassic, so if correctly assigned, the Devonian *Mcmurdodus* is by far the oldest known neoselachian (Cappetta et al., 1994). Turner (1995) redescribed the thelodontids, erecting *Turinia gavinyoungi*, and listed an associated fauna of shark scales, onychodont teeth, sarcopterygian scales, lepidotrichia, and acanthodian remains including elimatiid spines and *Acanthodes*-type and *Machaeracanthus* scales.

Turner (1991) and Young (1993) noted microvertebrate assemblages described by Turner et al.
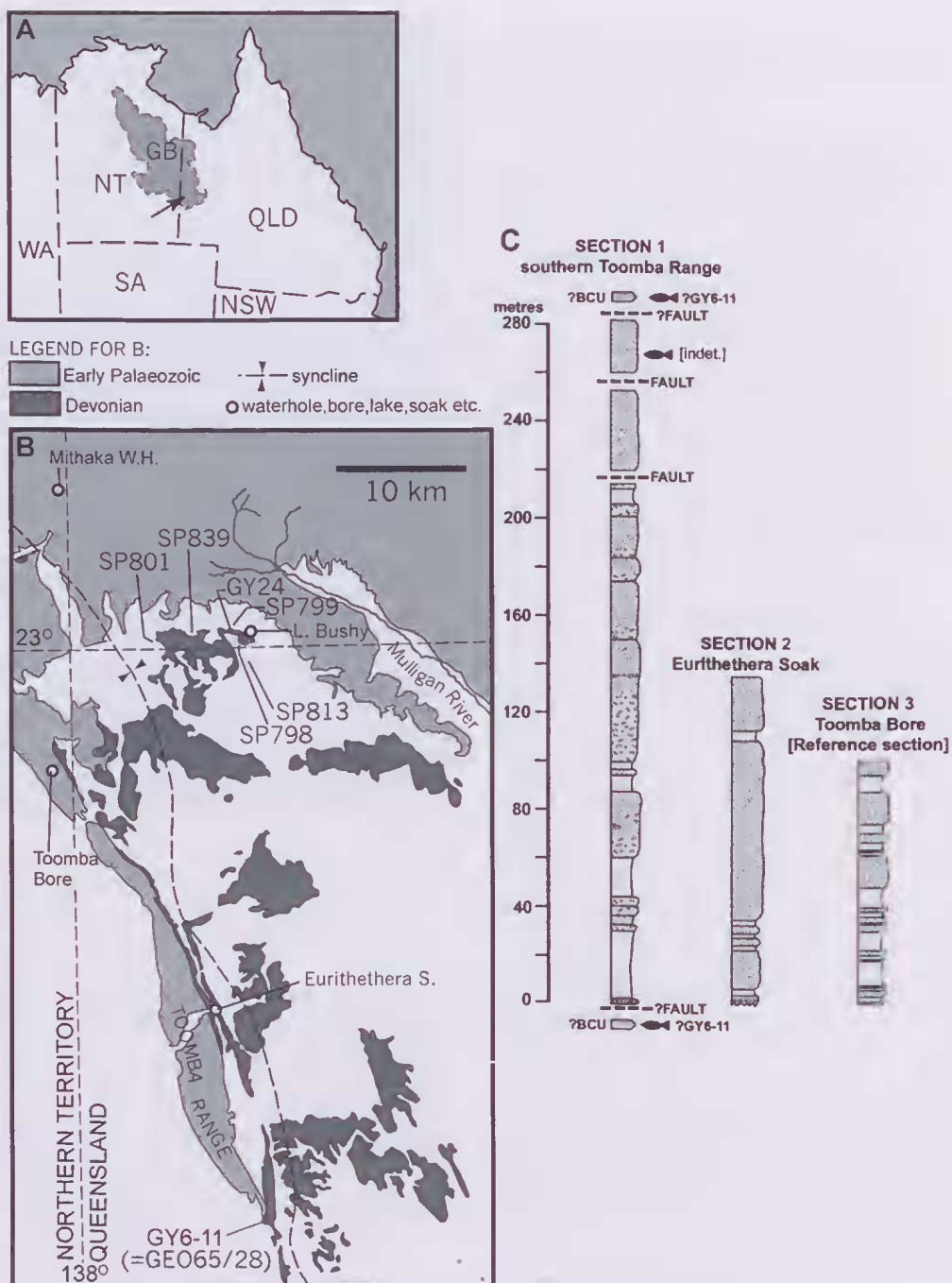
FIG. 1. A, Georgina Basin (GB) northern Australia; location of B indicated by arrow. B, S part of the Toko Syncline, geology from Hay River-Mt Whelan Special 1:250 000 sheet (Shergold, 1985), location of GY fossil localities collected 1977, and approx. localities for shot-point samples (prefix SP). GY24; locality for indeterminate spine (Young & Goujet, 2003). C, 3 measured sections through Cravens Peak Beds, modified from Draper (1976: fig. 4), and Turner et al. (1981: fig. 3): Section 1, S Toomba Range, about 100m S of GY6-11 (Fig. 1B), Section 2, Eurithethera Soak (see text for stratigraphic; Section 3, reference section of Smith (1972) as modified by Draper (1976), about 100m E of Toomba Bore.

(1981) contained conflicting evidence of age, and Young (1995: 20) discussed the possibility that the assemblage could have mixed material from older (shot-point samples) and younger (outcrop) horizons. Young (1996: 103) considered the basal calcareous unit of the Cravens Peak Beds to include a component younger (Eifelian) than the Early Devonian age assigned by Turner et al. (1981). Young & Turner (2000: fig. 4) gave alternative late Pragian-Emsian, or late Emsian-Eifelian, ages for the assemblage. Turner (1995, 1997) compared thelodontids from the outcrop with younger (Middle Devonian) turiniid scales from the Broken River Province, Queensland and the Aztec sequence of Victoria Land, Antarctica.

Turner et al. (1981) originally assigned the acanthodian fish scales to two taxa (*Nostolepis* sp. and *Gomphonchus* sp.), but examination of other remains, including spines and ossified scapulocoracoids, suggested a younger element in the fauna (Burrow, 2002). We suggest that at least some of the samples from west of the Toko Range are of ?late Lochkovian to early Pragian age, and the samples from the Toomba Range might be late Emsian or Eifelian.

FIELD OCCURRENCE

Turner et al. (1981) dealt with material from five shot-point samples, but only one sample from the limestone outcrop. Shot-point samples, obtained during a 1963 seismic survey of the Toko Range for Phillips Petroleum, and first recorded by Jones (in Reynolds & Pritchard, 1964), were calcareous marl, processed by washing, not acid digestion. They included some Ordovician conodonts (probably reworked, or perhaps due to contamination; Turner et al., 1981: 53). This is circumstantial evidence that the shot-point localities were sampling the basal contact between the Devonian sequence and underlying Early Palaeozoic (P.J. Jones, pers. comm.). In contrast, the limestone is a solid rock, only broken down by normal acid digestion techniques, so there is a lithological difference between the two sources.

According to field data for the Georgina Basin Project held at Geoscience Australia in Canberra, the original limestone sample (74710577), assumed initially to be from the Early Ordovician Coolibah Formation, was collected by J.J. Draper on 8 August 1975 from an outcrop which 'occurs along a fault'. Draper (1976: 3) stated that the outcrop occurred 'at the base of the scarp at the SE end of the Toomba Range; this outcrop has an area of about 5m² along a spur fault of the Toomba Fault'. He originally considered it to be probably unconformable on the Ordovician Mithaka Formation and to be unconformably overlain by sandstone and conglomerate of the Cravens Peak Beds, but later reinterpreted this to be a conformable contact (Turner et al., 1981). A 280m thick measured section of Cravens Peak Beds situated 100m south of the limestone outcrop begins with a basal pebbly unit (Draper, 1976: fig. 4, section 1), and the limestone occurs in gullies only about 10m from similar strata assumed to be the base of the Cravens Peak Beds (see Young & Turner, 2000: 464). However, an alternative interpretation is that the whole sequence is overturned, i.e. younging to SW, not NE. At least two faults were identified higher up in Draper's measured section (beneath the 220 and 260m levels; Draper, 1976: fig. 4), but these were omitted from the published section (Turner et al., 1981: fig. 3). The faulted contact noted in the original field assessment places uncertainty on the stratigraphic relationship between the two lithologies. Field observations (GCY, 1977) noted a nearby 'basal' conglomerate of the Cravens Peak Beds, but there are conglomeratic beds at many levels within the measured sections, so this evidence is not compelling. In addition, the supposed contact between clastics and limestone is parallel to mapped faults in the vicinity, consistent with it being an unrecognised fault. The (assumed) top of section 1 of Draper (1976) finishes in non-exposure; the only fossils are one poorly preserved fish sample showing a faint impression of tuberculate ornament, and a possible arthropod impression, collected within 20m of the (assumed) highest exposure. However, in the reference section for the Cravens Peak Beds at Toomba Bore (Draper, 1976: fig. 4, section 3), the only fossil (a plate impression from the placoderm *Wuttagoonaspis* sp.) occurs at the base. Many localities yielding a diverse fish assemblage including *Wuttagoonaspis* sp. (Young & Goujet, 2003) also occur in the lower part of the sandstone sequence. Field work is required to re-examine the outcrop relationships between Devonian limestone and sandstone in this area, but the geological information just summarised provides circumstantial evidence consistent with recognition of different acanthodian faunas in the limestone and the shot-point samples. Two alternative stratigraphic positions for the 'basal calcareous unit' (BCU) are indicated in Section 1 of Fig. 1C.

Of eight taxa originally documented from the 'basal calcareous unit', five were listed by Turner

et al. (1981: fig. 4) as common to the limestone and shot-point samples, but two thelodont taxa from the former were reassigned to a single new species by Turner (1995). The best preserved ostracods (*Healdianella* and *Bashkirina*?) come from the shot-point samples, and the cridostracan *Cryptophyllus* is best represented only from the limestone sample (Turner et al., 1981: fig. 15). Given the possibility that different levels may have been sampled, the poorly preserved unfigured remains of these crustacean taxa are in need of restudy (P.J. Jones, pers. comm.).

Young & Goujet (2003) concluded that the *Wuttagoonaspis* fauna from the Cravens Peak Beds and lower Dulcie Sandstone in the Georgina Basin was probably no older than Pragian, and no younger than early Eifelian, consistent with the suggested stratigraphic position of the limestone. Whether this *Wuttagoonaspis* fauna is younger or older than the *W. fletcheri* Ritchie, 1973 fauna in the type area in the Darling Basin, NSW (Mulga Downs Group) must await detailed analysis of faunal associations from many known but unstudied fish localities. The *Wuttagoonaspis* assemblage in the Darling Basin is recorded from many sites in the vicinity of the type locality (Wuttagoona Station, about 60km NW of Cobar), plus some 150km to the S (Glen et al., 1987; Young, pers. obs.), and some 360km to the W, in the Barrier Ranges north of Broken Hill (Coco Range Formation; Neef et al., 1995). Correlation of these widespread localities is uncertain without detailed systematic work, but we note a range of undescribed acanthodian material from various localities and cores in the Darling Basin which represent at least several horizons.

OTHER LOCALITIES

UQL4697 = BRJ103A. Section ~70m west of old road crossing of Digger's Creek; stratigraphically below Fish Hill limestones; Bracteata Formation, ?late Emsian-early Eifelian.

UQL4704 = BRJ104B. Mid-level in section/traverse along limestone outcrop from Digger's Creek Crossing to road; GR 683 489 Burges 1:100000 sheet; Bracteata Formation, late Emsian, probably *serotinus* or *patulus* CZ.

BRJ133K. Jessey Springs; Chinaman Creek Limestone, late Emsian/Eifelian.

Abbreviations. ANUV, Gavin Young collection, Australian National University; BMR, Bureau of Mineral Resources, now Geoscience Australia; BRJ, J. Jell Broken River Formation collection; CPC, Commonwealth Palaeontological Collection, Canberra; CZ, Conodont Zone/s; GY, Gavin Young sample localities from 1977

collecting; L, Natural History Museum collection, Prague; SP, shot-point localities; UQL, University of Queensland Earth Sciences locality; UQY, University of Queensland Earth Sciences (Queensland Museum) collection.

SYSTEMATIC PALAEONTOLOGY

Class ACANTHODII

REMARKS. Nostolepis has usually been assigned to the Climatiiformes Berg, 1940, now considered to be a paraphyletic group (Janvier, 1996). Also, scales with *Nostolepis*-type histology have been described on articulated fish with dentigerous jaw bones (Valiukevicius, 2003), indicating they should be assigned to the Ischnacanthiformes. These new taxa thus also throw doubt on the familial assignment of *Nostolepis*, which was erected for isolated scales. For these reasons, we have not assigned *Nostolepis* to an order or family.

Nostolepis Pander, 1856

TYPE SPECIES. *Nostolepis striata* Pander, 1856.

Nostolepis sp. cf. N. striata
(Fig. 2A,B)

MATERIAL. One scale CPC20088/3 from SP799 (?*pesavis/sulcatus* CZ, ?late Lochkovian/early Pragian).

DESCRIPTION. Light amber coloured, about 1.0mm long, with about four crown ridges rising up from the short, slightly-inclined neck anteriorly. Main central plane of crown horizontal, smooth behind ridges; a narrow, lower ledge is preserved on one side. Scale base bowl-shaped, moderately swollen. Posterior crown and base have been broken off.

REMARKS. The scale is one that Turner et al. (1981: 60) referred to as "scales ... resemble *Nostolepis striata*". Based on morphology, the scale is comparable to nostolepid scales also assigned to *Nostolepis* sp. cf. *N. striata* from the Martins Well Limestone (?*pesavis/sulcatus* CZ) of the Broken River region, north Queensland (Turner et al., 2000; Burrow, 2002).

Order ISCHNACANTHIFORMES Berg, 1940
Family PORACANTHODIDAE Vergoossen, 1997

Radioporacanthodes Vergoossen, 1999
Radioporacanthodes sp.
(Fig. 2C,D)

MATERIAL. Two scales CPC20088/1 (Fig. 2C; figured as *Nostolepis* sp. in Turner et al., 1981: fig. 14D) and

CPC20088/2 (Fig. 2D), from SP799 (?*pesavis/sulcatus*, ?late Lochkovian/early Pragian).

DESCRIPTION. Scales amber-coloured; CPC20088/1 1.0mm wide; CPC20088/2 0.7mm wide; crowns flat, horizontal. CPC20088/2 with about eight short weakly-developed ridges along the anterior crown margin; most of this area on CPC20088/1 is broken off. Posterior crowns broken off on both scales. Necks deep, concave and about the same depth all round. Short vertical slits score neck just above the base/neck junction anteriorly and high on the neck posteriorly. Bases strongly convex forward of centre, protruding markedly in front of crown, tapering towards the posterior corner.

REMARKS. Although diagnostically important posterior crown regions have broken off the scales, they compare closely in all other respects with *Radioporacanthodes* sp. from Martins Well Limestone (?*pesavis/sulcatus* CZ; Turner et al., 2000; Burrow, 2002). Some Lochkovian scales of *Gomphonchoporus hoppei* (Gross), 1971 and *R. porosus* (Brotzen), 1934, and scales from the Pridoli and Lochkovian of the East Baltic and Byelorussia which Valiukevicius (1998: pl. 7.4) assigned to "*Gomphonchus sandelensis* or *Poracanthodes punctatus*", are also similar.

Order ACANTHODIFORMES Berg, 1937

REMARKS. Berg (1940) listed seven orders within the Acanthodii: Climatiiformes, Ischnacanthiformes, Gyracanthiformes, Diplacanthiformes, Acanthodiformes, Cheiracanthiformes, and Mesacanthiformes. Miles (1966) and Novitskaya & Obruchev (1967) demoted the latter three monofamilial groups to families within one order. Presumably to avoid confusion with Berg's groups, Novitskaya & Obruchev (1967) used the '–ida' suffix rather than '–iformes' for acanthodian orders, but present consensus favours reverting to the '-iformes' suffix. Acanthodiformes thus comprises Mesacanthidae, Cheiracanthidae and Acanthodidae. According to Denison (1979), this familial division was based on gradual transition from 'primitive' to specialised states, without clearcut diagnostic characters. Denison placed all relevant species in Acanthodidae, because of this perceived lack of clearcut boundaries between the groups. However, some characters of the families (cf. Miles, 1966) are not transitional. Mesacanthids have one pair of intermediate spines and smooth scales, characters which are plesiomorphic for the order,
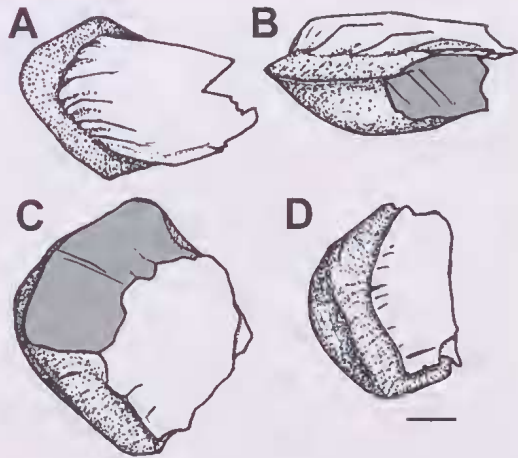

FIG. 2. Acanthodian scales from SP799. A-B. *Nostolepis* sp. cf. *N. striata* scale CPC 20088/3. A, crown view; B, lateral view. C-D. *Radioporacanthodes* sp. scales. C, CPC 20088/2 crown view; D, CPC 20088/3 crown view. Anterior is to left, scale bar = 0.2mm.

but also have synapomorphies including blade-like hyoidean gill covers and a mandibular splint (Hanke & Wilson, 2004: app. 1,2). All cheiracanthids have ornamented scales and lack intermediate spines; and all acanthodids have smooth scales, erectile pectoral spines, either unpaired or no pelvic spines and no intermediate spines. Zajic (1995) redefined Acanthodidae to exclude *Howittacanthus*, and erected Howittacanthidae, diagnosed by paired pelvic spines, smooth scales and lack of intermediate spines. However, paired pelvic spines is a plesiomorphy, and the Acanthodidae also have smooth scales and lack intermediate spines.

Family MESACANTHIDAE Moy-Thomas, 1939

Teneracanthus gen. nov.

TYPE SPECIES. *Teneracanthus toombaensis* sp. nov.

ETYMOLOGY. Latin: *tener*, delicate; and the common suffix used for acanthodian taxa: *acanthus*, thorn or spine.

DIAGNOSIS. Acanthodiform acanthodian; scapulocoracoid with a long, slender scapular shaft having a circular cross-section, a lateral wide-based, triangular scapular blade which is about one-quarter the height of the scapular shaft, and a medial coracoid blade of similar shape which diverges at ca. 45° to the axis of the shaft; scapulocoracoid articulates with the trailing and lateral sides of the proximal end of the pectoral

TABLE 1. Comparison between five mesacanthid taxa.

	Lodeacanthus gaujicus	*Mesacanthus mitchelli*	*Melanoacanthus minutus*	*Teneracanthus toombaensis* gen. et sp. nov.	*Triazeugacanthus affinis*
longitudinal ribs on fin spines	deep anterior groove, fine post. grooves	deep anterior groove, fine post. grooves	none	deep anterior groove, some with fin post. grooves	2-3 shallow grooves
denticulations on fin spine	juveniles- distal half of leading edge; adults- none except on intermediate spines	none	none	distal half of leading edge on pectoral spines	none
longitudinal cleft, proximal pectoral spine	yes	no	?	yes	?
fin spine insert base	short	short	short	short	short
scapulocoracoid/ pectoral fin spine articulation	scapulocoracoid blades dorsal and lateral to pectoral spine	pectoral spine lateral to coracoid blade	?	scapulocoracoid blades dorsomedial and lateral to pectoral spine	scapulocoracoid blade ?dorsolateral to pectoral fin spine
cross-sectional shape of scapular shaft	juveniles- flat; adults- circular	circular	?	circular	circular
height of expanded scapulocoracoid blade: total scapulocoracoid height	1:5	2:3	1:2	1:5	1:4
shape of scapulocoracoid blade	short-based triangle	? triangle	short-based triangle	long-based triangle	short-based triangle
procoracoid	none	none	none	none	none
palatoquadrate	single growth centre; fenestrated	two growth centres; no fenestra	?	?	?
branchiostegal rays	mid-sized, curved, outer face with single fine longitud. ridge	long, ornamented	long	?	short, some forked and some pointed
ceratotrichia	none	?none	?none	?	round, forked
tectal tesserae	edging infraorbital sensory line	cover head	cover head	?head and sensory line	cover head
size of flank scales	7/mm	16/mm	'small'	4-5/mm	5/mm
scale crown	smooth	smooth	smooth	smooth	smooth
scale base	juveniles – concave; adults - conical	rounded convex	'tumid'	pyramidal	relatively flat
scale histology	?	pulp canals, orthodentine	*Acanthodes*-type?	*Acanthodes*-type but no interconnecting network	?

fin spine, astride its longitudinal cleft; small rounded 'glenoid' process postcromedial to base of scapular shaft; no procoracoid; pectoral fin spines bear fine denticulations on the distal half of the leading edge; fin spines are slightly curved, with one deep longitudinal groove separating the rounded ridge which forms the leading edge from the main body of the spine; the sides of some non-denticulated (?median) spines bear fine longitudinal ridges proximally; some symmetrical fin spines with basal cartilages; fin spines have a relatively wide central pulp cavity, a network of fine dentine tubules leading into vascular canals which run more or less longitudinally; tri-basal pectoral fin; smooth-crowned scales of two types: normal flank scales with a

square crown, concave neck and a base shaped like an inverted pyramid, and probable caudal scales with an elongated crown, negligible neck, and a shallow, diamond-shaped base; scales have *Acanthodes*-type histology but lack a fine network of processes between centripetal dentine tubules in the crown.

Teneracanthus toombaensis gen. et sp. nov.
(Figs 3A-E,4A-T,5A-K,6D-F; Table 1)

1981 '*Gomphonchus?* sp.' Turner et al.: fig. 14A-C
1981 'acanthodian spines' Turner et al.: 60
1987 'smooth ischnacanthid scales' Young et al.: 239
1995 'climatiid spines' Turner: 683
1995 '*Acanthodes*-type scales' Turner: 683
2000 'new mesacanthid' Young & Turner: 464
2003 'Acanthodian remains', in part Young & Goujet: 9

ETYMOLOGY. For the Toomba Range.

MATERIAL. HOLOTYPE: ANUV2940 (Figs 3A-C,4R-S), pectoral fin spine attached to a scapulocoracoid; Locality GY11, Toomba Range, western flank of Toko Syncline, Georgina Basin, western Queensland (Fig. 1A,B). PARATYPES: left scapulocoracoid ANUV2969.2 (Figs 3D-F,4C-D), pectoral fin spine ANUV2969.1 (Fig. 4L-M), fin spine ANU V2969.5 (Fig. 4K), fin spine ANUV2969.6 (Fig. 4P-Q). ADDITIONALMATERIAL: One right scapulocoracoid articulated with pectoral fin spine, one left pectoral fin spine, 13 fin spine fragments, one ground thin section from fin spine fragment, one left and one right scapulocoracoid, two scapulocoracoid shaft fragments, one ?pharyngobranchial, and 47 scales in samples ANU V2937-41 from GY11; one left and one right scapulocoracoid, fin spines, branchial elements, scales, and a left palatoquadrate in ANUV2969 from GY11; seventeen scales including CPC20087/1 and CPC20087/2 and two ground thin sections, in BMR sample 74710577 from locality GEO 65/28 (Turner et al., 1981); all from the Cravens Peak Beds. One scale in BRJ103A and 16 scales in BRJ104B (Fig. 5K), Bracteata Formation, and ?one scale in BRJ133K, Chinaman Creek Limestone, Broken River Group.

DIAGNOSIS. As for genus.

GEOGRAPHICAL & STRATIGRAPHIC DISTRIBUTION (AUSTRALIA). Cravens Peak Beds (?late Emsian/early Eifelian), Georgina Basin, western Queensland (Fig. 1A-C); Bracteata Formation and possibly Chinaman Creek Limestone (late Emsian/early Eifelian), Broken River Group, north Queensland.

DESCRIPTION. *Scapulocoracoids* (Figs 3D,4A,B). Samples from GY11 include four scapulocoracoids, two left and two right. ANUV2939.5 (Fig. 4A) is an element from the right side, 2.5mm high, with a long thin scapular shaft having a circular cross-section of 0.4mm diameter, expanding to a thin wide-based lateral scapular blade with a stretched-triangular shape; the blade is 1.5mm long x 0.5mm high anteriorly. A rounded medial knob at the base of the scapular shaft is possibly a glenoid process. ANUV2969.8 (Fig. 4B) is a left scapulocoracoid, 3.6mm high. ANUV2939.6 is a left scapulocoracoid, 5mm high, with only the upper part of the lateral scapular blade preserved. Paratype ANUV2969.2 (Figs 3D-E,4C-D) is a right scapulocoracoid, 2.7mm high, with the scapular shaft, ?glenoid process, medial coracoid and lateral scapular blade all preserved. Some delicate perichondral granular mineralisation is preserved anteriorly, with no indication of a coracoid process or procoracoid.

Denticulated fin spines (Fig. 4H,L-Q). ANUV 2939.10 (Fig. 4N) is an almost complete, but fragmented, pectoral fin spine, 11mm long, curving slightly, and is from the left side; the main shaft has a circular cross-section and smooth sides, with a longitudinal ridge along the leading edge. The distal half to two-thirds of this ridge bears fine backward-pointing denticulations. The proximal end of the spine has a thin film of ossified cartilage across the triangular cleft between the two sides of the spine. This spine possibly articulated with the left scapulocoracoid described above. ANU-V2939.11 is a right pectoral fin spine, 11mm long but missing the proximal part; it is otherwise comparable to the left pectoral fin spine, having a circular cross-section and distal denticulations. These pectoral fin spines are not exactly symmetrical dorso-ventrally, having a smooth transition from the leading edge ridge to groove to main body of spine on one side, but with an abrupt, 'stepped-down' transition from the ridge to the main body of the spine on the other side. Paratype ANU V2969.6 (Fig. 4P-Q) is a complete, laterally flattened fin spine 14mm long, also showing slight longitudinal curvature. The pulp cavity is open along the proximal half of the trailing edge, and the distal half of the leading edge is denticulated. Other fin spine material in the samples includes short fragments of denticulated spines, including one in ANUV2941 and three in ANUV2939 (Fig. 4H). Paratype ANUV2969.1 (Fig. 4L-M) is the proximal 3mm of a ?pectoral fin spine which has a delicate sheet of perichondral ossification preserved across the longitudinal cleft. This sheet has three holes, each 0.2-0.3mm long: a proximal pair and a more distal single central hole, which probably represent the articulation points of the fin radials, showing that these fin elements were arranged in a triangle rather than linearly.

Non-denticulated fin spines (Figs 3G,4E-G,K). Paratype ANUV2969.5 (Fig. 4K) is a complete, symmetrical? spine 12mm long, with a smooth leading edge ridge and several (up to five) fine longitudinal ridges on each side. A delicate sheet of perichondral ossification is partly preserved boxing over the open pulp cavity of the proximal half of the spine, and is presumed to have covered the basal cartilage of the fin. As the spine is symmetrical, and dorsal fins are the only median fins for which basal cartilages have been recorded in any acanthodians, the spine is probably from the dorsal fin. Two fragments from sample ANUV2939 are proximal ends of spines,
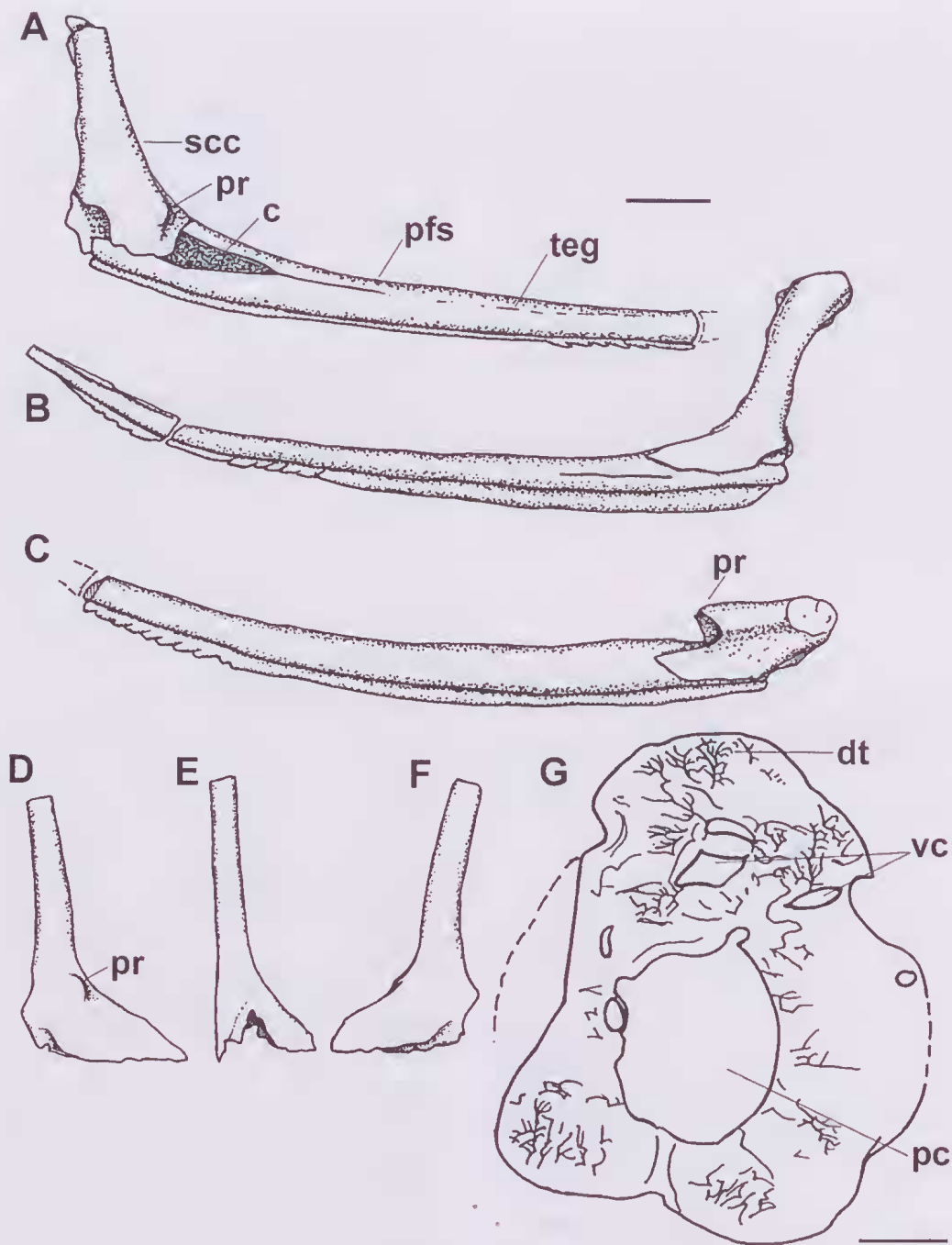
FIG. 3. Drawings of pectoral girdles and fin spine of *Teneracanthus toombaensis* gen. et sp. nov. from site GY11. A-C. Articulated right scapulocoracoid and pectoral fin spine ANU V2940. A, medial view, B, lateral view, and C, dorsal view. D-F. Right scapulocoracoid ANU V2969.2, in D, medial view, E, anterior view, and F, lateral view. G. ground thin cross-section of fin spine ANU V2939.9. Scale bar = 1.0mm in A-C, 0.5mm in D-F, 0.1mm in G. c, spine cleft; dt, dentine tubules; pc, pulp cavity; pfs, pectoral fin spine; pr, ?glenoid process; teg, trailing edge groove; vc, vascular canals.
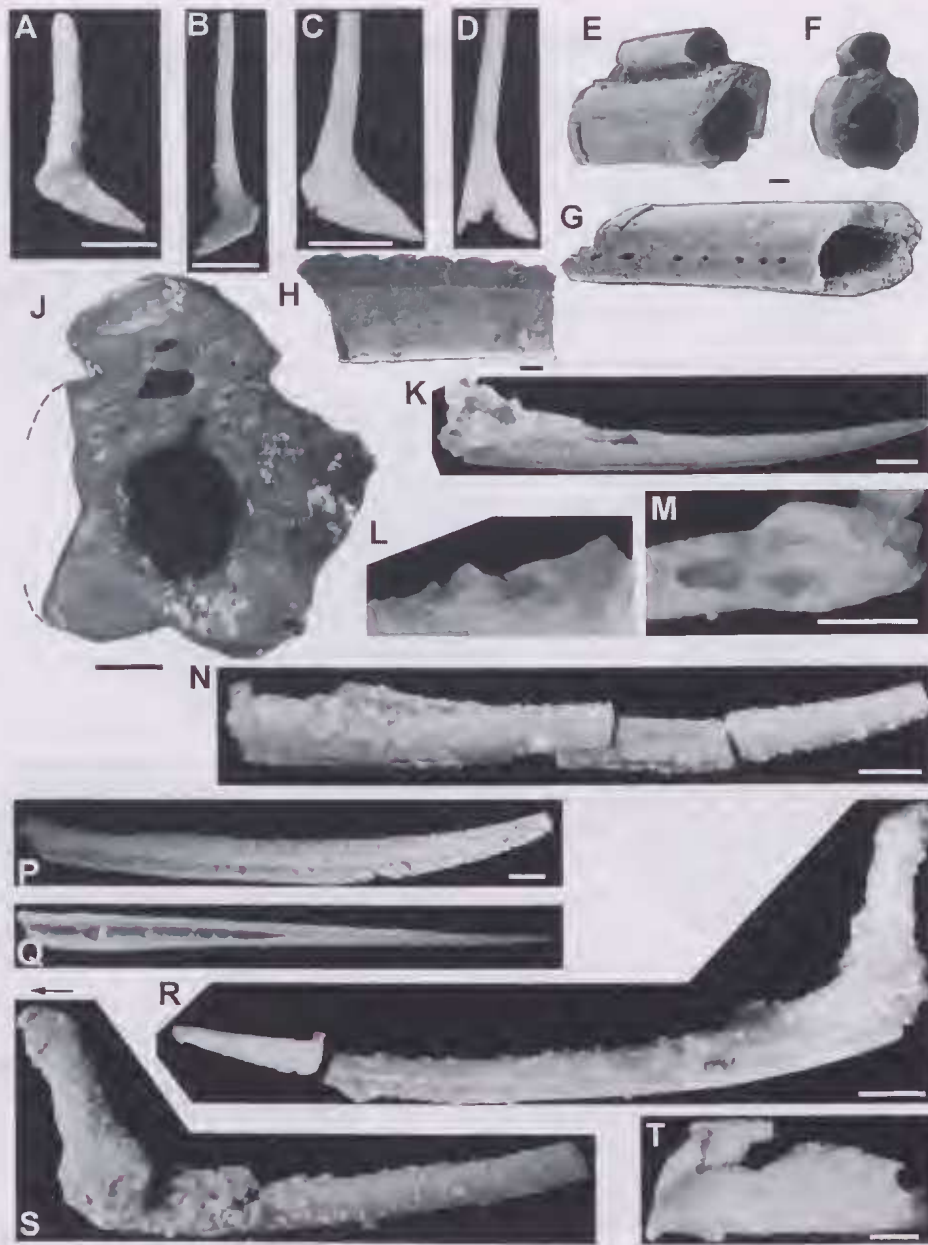
FIG. 4. Pectoral girdles, fin spines and palatoquadrate of *Teneracanthus toombaensis* gen. et sp. nov. from GY11. A, right scapulocoracoid, medial view ANUV2939.5; B, left scapulocoracoid, lateral view ANUV2969.8; C-D, right scapulocoracoid, medial and anterior views ANUV2969.2; E-G, non-denticulated spine fragment ANUV2939.8 E, lateral view. F, end-on view, and G, latero-basal view; H, lateral view denticulated fin spine fragment ANUV2939.7; J, transverse section ANUV2939.9, under cross nicols; K, median fin spine ANUV2969.5, showing perichondral ossification of basal cartilage; L-M, proximal cleft of pectoral fin spine ANUV2969.1, showing three holes in the perichondral ossification; N, ?left pectoral fin spine ANUV2939.10, dorsal view; P-Q, denticulated fin spine ANUV2969.6 P, lateral view, and Q, trailing edge view, R-S, articulated right scapulocoracoid and pectoral fin spine ANUV2940, R, lateral view, and S, medial view; T, fractured perichondral ossification of left palatoquadrate ANUV2969.4. Scale bar=1mm in A-D, K, N-S, 0.5mm in L-M, T, and 0.1mm in E-J; arrow to anterior.
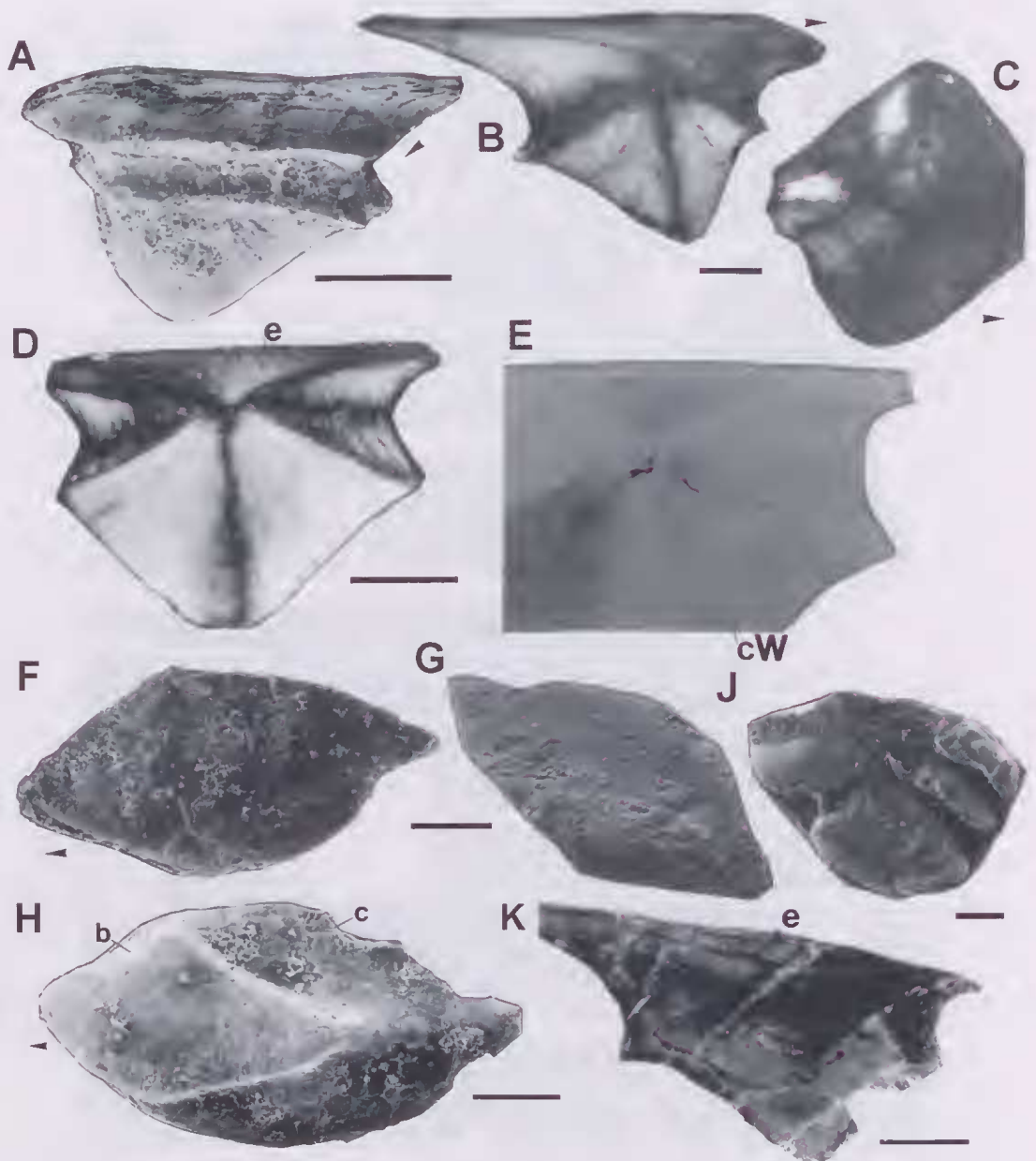
FIG. 5. Scales of *Teneracanthus toombaensis* gen. et sp. nov. from GY11 (A-J) and BRJ104B (K). A, antero-lateral view flank scale ANUV2939.12; B, vertical longitudinal section flank scale, ANU V2939.13, under cross nicols; C, horizontal section crown flank scale ANUV2939.14, under cross nicols; D, E, vertical transverse section flank scale ANUV2939.15, D under cross nicols; F, G, caudal scale (*sciotoensis* var.) ANUV2937.8, F, crown view, G, latero-crown view; H, caudal scale ANU V2939.16, basal view; J, ?cheek tessera ANUV2939.17, crown view; K, Vertical longitudinal section flank scale UQY9335. Scale bar=0.1 mm; arrow is anteriad; b = base, c =crown, cW =canals of Williamson, e = enameloid.

with part of the short striated insertion area preserved, and a wide open main central cavity. Most other fragments are short (Fig. 4E-G); two of the longer pieces are a mid-spine section, 4.2mm long, and a very slender distal fragment which is 2.5mm long. These are straight, laterally flattened, without denticulations and with two or more very fine longitudinal ribs per side on the main shaft of the spine. Irregularly-spaced rounded pores pierce the trailing edge groove (Fig. 4G).

Scapulocoracoid plus pectoral fin spine (Figs 3A-C,4R-S). Holotype ANUV2940, a fin spine, 12mm long, articulated with a scapulocoracoid, 3mm high (although the top of the shaft is broken off). Specimen heavily encrusted with small ?sand grains, obscuring finer details. Scapular shaft narrow with circular cross section. Scapulocoracoid attached to dorsal and lateral faces of the pectoral fin spine, with the straight ventral margin of the scapular blade paralleling the main longitudinal groove between the leading edge ridge and the main shaft of the spine. Medial coracoid blade of scapulocoracoid incomplete.

Spine histology (Figs 3G,4J). A wide central cavity extends through the length of the main shaft of the spine, with one or more longitudinal canals in the leading edge ridge. Other vascular canals are also visible, and denteons are developed near the central cavity and the vascular canals. Bone cell lacunae and lacunal widenings in dentine are lacking, with the hard tissue being relatively densely-branching, fine dentine tubules. A thin inner lamellar layer lining the central cavity is possibly present.

Palatoquadrate (Fig. 4T). ANUV2969.4, 2.8mm long, greatest height ca. 1.2mm, represents delicate, hollow perichondral granular mineralisation of most of a left upper jaw. A semicircular notch on the anterior edge resembles the embayment at junction of the metapterygoid and autopalatine cartilages on *Acanthodes bronni* (e.g. Miles, 1965: fig. 1A) and at the junction of the anterior and posterior parts of the palatoquadrate on *Mesacanthus mitchelli* (Watson, 1937), but there are no signs of separate ossification areas. Most of the palatoquadrate is preserved, including posterior part of the extrapalatoquadrate ridge and the hyomandibular groove, and the jaw joint articulation surface comprising prearticular and articular processes. Posterior edge of palatoquadrate almost vertical; anterodorsal part of the element missing, and thus presence or absence of a fenestra comparable to that in

Lodeacanthus (Upeniece, 1996: fig. 1B,C) is unknown.

Scale morphology (Figs 5A,F-H). Translucent, amber to cream coloured, small with smooth flat crown. Square-crowned (Fig. 5A) 0.2 to 0.3mm wide and long, with concave neck and base with a central pointed, inverted pyramid-shaped swelling surrounded by a relatively flat perimeter. Elongated scales are 0.2mm wide and 0.3 to 0.4mm long, with a short neck, and a flat or slightly convex diamond-shaped base.

Scale histology (Figs 5B-E,K,6D-F). Thick enameloid is developed through the centre of the crown, with long ascending dentine tubules in the anterior and posterior crown; these tubules show minimal branching. There are no bone cell lacunae in the base or crown. A network of Williamson's canals penetrates the base.

REMARKS. The tall slender scapular shaft with its circular cross section and the smooth-crowned scales with *Acanthodes*-type histology indicate the elements derive from an acanthodiform acanthodian. Fin spines and scapulocoracoids of *Teneracanthus toombaensis* gen. et sp. nov. are similar to *Cheiracanthus* spp. in the shape of scapulocoracoids, type of articulation between scapulocoracoid and fin spine, and the structure of the fin spines. The shoulder girdle/pectoral fin spine arrangement is unclear in other cheiracanthids (i.e. acanthodiforms with ornamented scales); eg., *Carycinacanthus* (Novitskaya & Obruchev, 1967), *Proto-gonacanthus* and *Homalacanthus* (Miles, 1966). Whereas the reconstructions of *Cheiracanthus murchisoni* Agassiz, 1835 (1833-43) and *C. latus* Egerton, 1861 in Watson (1937: figs 12,13) have the pectoral fin spine detached from the scapulocoracoid, Miles (1973; also Egerton, 1861) indicated that these elements were articulated. In *Cheiracanthus*, the scapulocoracoid shaft leans slightly forward and has a circular cross section. The ventral blade widens out below the shaft, forming a triangular region with a long straight ventral margin (Miles, 1973: 157, text-fig. 22). The scapulocoracoids of *Teneracanthus toombaensis* gen. et sp. nov. share these features, but also have a medial blade of similar shape to the lateral blade, so that the element straddles the proximal end of the pectoral fin spine. Also, *Cheiracanthus* differs by having a procoracoid anterior to the scapulocoracoid and pectoral fin spine (although lacking a procoracoid process on the scapulocoracoid). No procoracoid is preserved on the
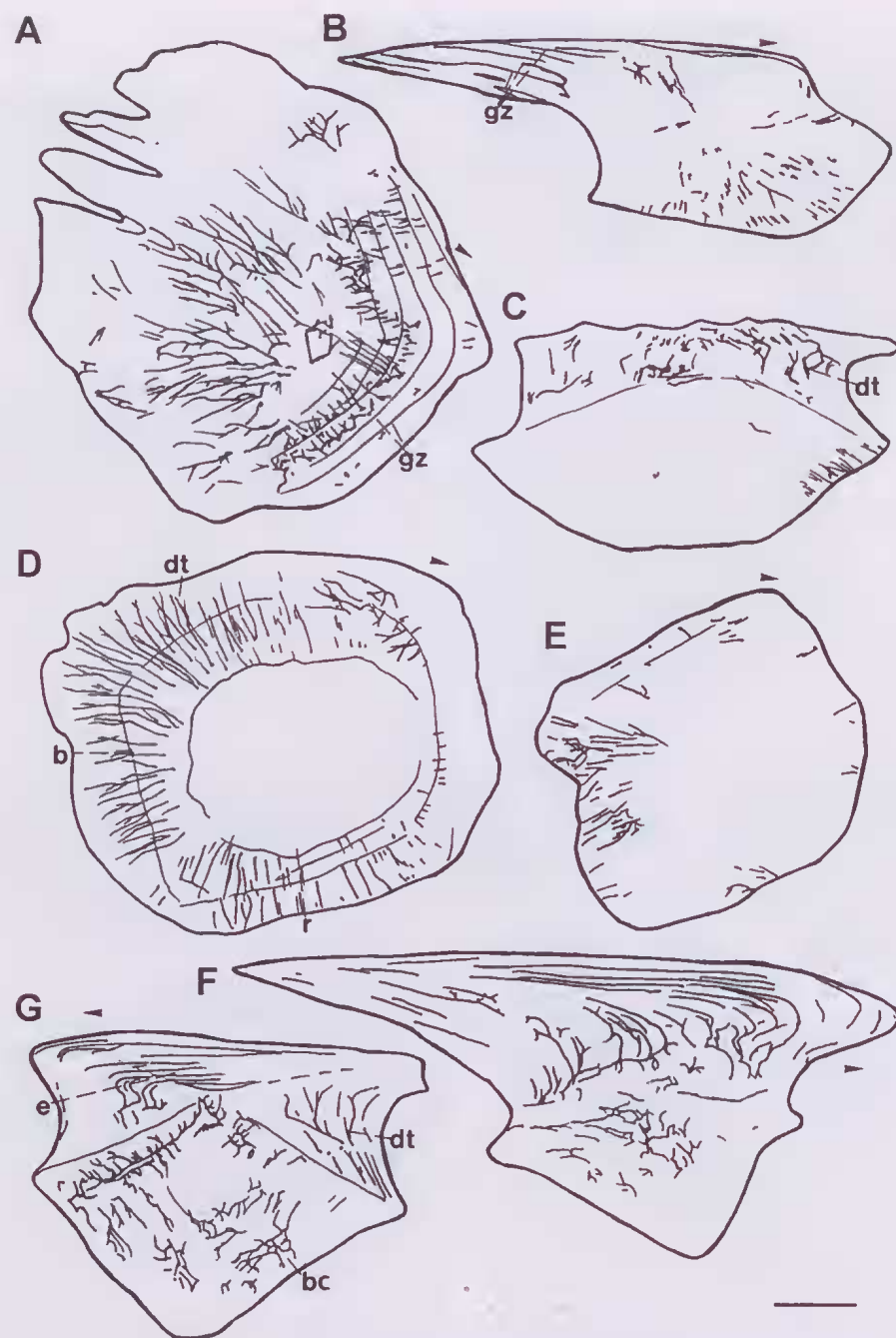
FIG. 6. Drawings of thin sections of scales from GY11. A-C, *Machaeracanthus pectinatus* sp. nov., ground thin sections. A, horizontal section crown ANUV2939.1; B, vertical longitudinal section ANU V2939.2; vertical transverse section C,ANUV2939.3. D-G, *Teneracanthus toombaensis* gen. et sp. nov. D, scale CPC20087.2 in anise oil; E-G, ground thin sections: E, horizontal section crown ANUV2939.4; F, vertical longitudinal section ANUV2939.13 ; G, vertical transverse section ANUV2939.15. Scale bar =0.1mm in A-F, 0.05mm in G; arrow to anterior; bc = cellular processes, dt =dentine tubule, gz growth zones.

Cravens Peak specimens, and the relatively complete scapulocoracoids have a smooth anterior face. Unlike cheiracanthids, which all have scales with ornamented crowns, the new taxon has the smooth-crowned scales which characterise the acanthodids and mesacanthids.

In acanthodids, the shoulder girdle structure and its articulation with the pectoral fin spine is well known in *Acanthodes bronni* (Lower Permian, Lebach, Germany). Unlike the new taxon, *Acanthodes* has a relatively short stout scapular shaft and an extensive coracoid flanking the fin spine medially, as does *Howittacanthus* (Long, 1986). Of mesacanthids (Table 1), *Mesacanthus mitchelli* (Egerton, 1861) from the Early Devonian of Scotland, has a simple scapulocoracoid attached to the inner face of the pectoral fin spine (Miles, 1973: text-fig. 23), and *Triazeugacanthus* Miles, 1966 from the Frasnian of Miguasha, Canada has a tall and anteriorly curved scapulocoracoid. Miles (1966) indicated that in *Triazeugacanthus* the scapulocoracoid was dorsal to the pectoral fin spine, but Gagnier (pers. comm.) suggested that it covers some of the 'inner' part of the pectoral fin spine.

The scapulocoracoid plus pectoral fin spine ANUV2940 complex is similar to that of the Emsian mesacanthid *Melanoacanthus minutus* Cumbaa & Schultze, 2002, but compares most closely with that of mesacanthid *Lodeacanthus guajicus* Upeniece, 1996 from the lower Frasnian Lode Formation of Latvia. Upeniece (1996) described articulated specimens of both juveniles and adults of *Lodeacanthus*, ranging from 13.6-38.9mm in length. The flank scales are smooth-crowned, with conical bases in adults but with concave bases in juveniles. The palato-quadrate on *Lodeacanthus* is ossified as a single unit and has a large fenestra anterodorsal to the jaw articulation; prearticular and articular processes extend from the ventral shelf. ANU V2969.4 shows a comparable structure, although with the fractured and incomplete preservation of the dorsal region the presence or absence of a fenestra is unclear.

The scapulocoracoid in *Lodeacanthus* has a scapular shaft with a circular cross-section in adults and flattened oval cross-section in juveniles; the shaft is 4/5 total height of the scapulocoracoid. As on *Teneracanthus*, the ventral part of the scapulocoracoid divides into two blades straddling the cleft of the pectoral fin spine. In *Lodeacanthus*, the fin spines have an elliptical cross section and lack insertion areas. The distal leading edge of all fin spines, except

intermediate ones, lack ornamentation in adults, but in juveniles all fin spines have a row of denticles on the leading edge. In the adults, the ratio of pectoral fin spine: total length of fish averages 0.15. By comparison, the *Teneracanthus toombaensis* gen. et sp. nov. fish which had the articulated scapulocoracoid/pectoral fin spine is estimated to have been about 73mm long.

All *Teneracanthus toombaensis* gen. et sp. nov. scales have convex bases, indicating (cf. *Lodeacanthus*) they are from an adult rather than a juvenile. It differs from *Lodeacanthus* in having denticulated pectoral fin spines on adult fish and long-based scapulocoracoid blades. It is uncertain whether *Teneracanthus* had pre-pelvic fin spines; none of the fin spine fragments appear to be from small spines comparable to the pre-pelvic spines of *Lodeacanthus*.

Scale histology for *Teneracanthus toombaensis* gen. et sp. nov. shows numerous centrifugal, non-branching dentine tubules in the upper crown, indicating *Acanthodes*-type histology similar to that in scales of *Cheiracanthus latus*. They differ to *Acanthodes bronni* (Gross, 1947: fig. 18B) in lacking the fine network between the long dentine tubules. Scales of *Mesacanthus* spp. from England and Scotland are much smaller than those of other mesacanthids, and often have relatively wide vascular canals piercing the base in caudal scales (CJB, pers. obs.). However, they do have long dentine tubules typical of acanthodiforms (Denison, 1979). No description was given of *Lodeacanthus* scale histology.

Smooth-crowned scales of late Early to Middle Devonian age have traditionally been referred to *Acanthoides* Wells, 1944 or *Acanthodes*? spp. Scales of *Teneracanthus toombaensis* gen. et sp. nov. resemble those from the Eifelian bone beds of Ohio, Indiana and Kentucky in the U.S.A. assigned to *Acanthoides dublinensis* and *A. sciotoensis* by Wells (1944) and Storrs (1987: fig. 3.5,6). Although the crown shape is comparable, scales of *Acanthoides* have rounded rather than pointed bases. From the same U.S. bone beds are the fin spine fragments which Wells (1944: pl. 2.46,47) assigned to *Gyracanthus*? *castmani*, and Storrs (1987: fig. 3.7) to 'acanthodian fin spine fragment', which resemble the denticulated spines of *Teneracanthus toombaensis* gen. et sp. nov. In Queensland, De Pomeroy (1996: fig. 3O,P) referred scales from the Papilio Formation (Givetian, mid *varcus* CZ) of the Broken River Province to *Acanthoides* sp. These were

described as having a 'highly convex' base, which presumably means a rounded base. However, several scales which have the distinctively pointed base like those of *Teneracanthus toombaensis* gen. et sp. nov. are present in late Emsian/?early Eifelian limestones of the Broken River region, and are assigned here to the same taxon (Fig. 8G).

Pectoral fin structure. The knob shaped process posteromedial to the base of the scapular shaft is comparable to the structure which Miles (1973: text-fig. 40B) designated a glenoid process in *Diplacanthus striatus* Agassiz, 1844.

Three-D preservation of delicate perichondral granular mineralisation at the base of the pectoral fin spine is a unique record of the structure of the fin base. Three basal radials have previously been noted in *Acanthodes bronni* (Miles, 1973: 153, text-fig. 20), but in that species the three stout elements articulate against the margoradialis of the scapulocoracoid, aligned linearly perpendicular to the fin spine. This arrangement is drastically different to that in *Teneracanthus*, where three presumably uncalcified radials apparently issued from the proximal cleft of the pectoral fin spine. The near-complete scapulocoracoid ANUV2969.2 has clearcut ventral edges to the lateral and medial blades, indicating that the coracoid did not extend further ventrally, and thus negating the possibility of a fin radial articulation comparable to that of *A. bronni*. All reconstructions of pectoral fin radials in the latter species place them in a straight line, perhaps influenced by comparison with extant actinopterygians and chondrichthyans, with their long-based fins. It is unlikely, however, that *A. bronni* had a short-based, triangular arrangement like that in *Teneracanthus*, as *A. bronni* had a long narrow margo radialis (Miles, 1973: pl. 14.2). Several climatiid taxa, e.g. *Sabrinacanthus arcuatus* (Miles, 1973: text-fig. 29) and *Ptomacanthus* sp. indet. (Miles, 1973: text-fig. 32), have cartilage spanning the proximal cleft of the pectoral fin spine, which Miles (1973) interpreted as the margo radialis. Although the acanthodian endoskeletal shoulder girdle has been described as a 'scapulocoracoid', most taxa lack a distinguishable coracoid region. Thus in most acanthodians, as exemplified by *Teneracanthus*, it seems likely that the pectoral fin endoskeleton (if present) articulated with the cartilage which filled or covered the proximal cleft of the pectoral fin spine.

Recognition of the triangular arrangement of the pectoral fin radials in *Teneracanthus* encouraged consideration of the pectoral fin base in some of the earliest 'true' chondrichthyans which lack paired fin spines. This region on the Carboniferous chondrichthyan *Hamiltonichthys mapesi* Maisey, 1989 was reconstructed with the three fin basals aligned linearly (Maisey, 1989: fig. 14). According to Maisey (1989: 19), "articulation with the scapulocoracoid is mainly protopterygial, although the mesopterygium and metapterygium may also have met the shoulder girdle". Goujet (2001) noted that in chondrichthyans with a tribasal fin, only one element articulates with the girdle, with the other basal elements just overlapping rather than articulating with the girdle. As it now seems clear that proto-chondrichthyans had pectoral fin spines (Wilson & Hanke, 1998; Miller et al., 2003), the linear tribasal arrangement in 'true' chondrichthyans is possibly related to the loss of the articulation cartilage in the cleft of the pectoral fin spine. What can we infer for the plesiomorphic condition in acanthodians? The Placodermi are generally regarded as the sister group of all other gnathostomes. Goujet (2001) proposed that a monobasal pectoral fin is a general condition within the gnathostomes, and is plesiomorphic for placoderms. This contradicts the previously held view that a monobasal fin is a synapomorphy of the sarcopterygians (Janvier, 1996), but is supported by embryological studies of zebrafish as well as by the structure of the chondrichthyan 'tribasal' fin (Goujet, 2001). Unfortunately, the internal skeleton of the fins in Acanthodii is usually not preserved, or poorly ossified, and is thus poorly known. Although the margo radialis has been identified in several climatiids, the only acanthodian other than *A. bronni* in which pectoral fin radials have been identified is *Ischnacanthus* Powrie, 1864. Watson (1937) described four pectoral fin elements, which Miles (1973) interpreted as radials, in a specimen of *I. gracilis* (NMS 1891.92.258), but the arrangement of these elements has not been detailed. We can only presume that, if the general condition in gnathostomes is a monobasal pectoral fin as proposed by Goujet (2001), then if we accept the current view of gnathostome phylogeny, the stem acanthodian would either have had a monobasal fin, or have descended from a derived stem-group gnathostome which had already developed a tribasal pectoral fin.

Order incertae sedis

Family MACHAERACANTHIDAE fam. nov.

TYPE GENUS. *Machaeracanthus* Newberry, 1857, thus far the only known member.

DIAGNOSIS. Acanthodian fishes lacking paired and median fin spines of typical acanthodian structure (i.e. with a pulp cavity opening out along the proximal part of the trailing edge of the spine); having only paired fin spines, derived from internal fin rays or radials; scales with both apposed and superposed crown growth zones; perichondrally ossified scapulocoracoid with a relatively slender scapular shaft broadening out to a sub-triangular scapulocoracoid blade.

Machaeracanthus Newberry, 1857

TYPE SPECIES. *M. peracutus* Newberry, 1857

REMARKS. Affinities of *Machaeracanthus* have been extensively debated over recent decades (Janvier, 1996), with some (e.g. Goujet, 1995) assigning the genus to the Chondrichthyes, others (e.g. Zidek, 1981) maintaining inclusion in Acanthodii (as first proposed by Fritsch, 1893), and yet others remaining equivocal (e.g. Mader, 1986, assigned *Machaeracanthus* to 'Gnathostomata incertae sedis'). The original material of *M. bohemicus* (Barrande, 1873) from the Pragian Dvorce prokop Limestone and the early Emsian Zlichov Formation of Bohemia included an uncatalogued specimen (Barrande, 1873: pl. 34.29-34) from the Dvorce prokop Limestone comprising fin spines associated with an ossified endoskeletal scapulocoracoid (the latter captioned as 'Ossement de nature indéterminée'). The part of the specimen has not yet been refound, but the counterpart (Barrande, 1873: pl. 34.33,34) was identified (by CJB) as specimen Lc 98 in the National Museum collection, Prague. As noted by Fritsch (1895) and Zidek (1975, 1981), this scapulocoracoid is comparable in shape and structure with those of climatiids and ischnacanthiforms. Gross (1973) assigned scales associated with *M. bohemicus* spines from the Lochkovian Radotin Limestone, Kosor to the taxon. These scales resemble those of poracanthodid scales in shape and ornament, but lack a pore canal system within the scale crown. Many of the fin spines have a calcified core; prismatic calcified cartilage was not associated with any of the specimens. As far as known, *Machaeracanthus* lacks features which indicate chondrichthyan affinity: no prismatic calcified cartilage, no loss of endoskeletal bone,

no pulp canals piercing scale bases, and no chondrichthyan-type teeth, although Goujet (1993) suggested that *Leonodus* Mader, 1986 teeth could be from *Machaeracanthus*. However, Soler-Gijón & Hampe (2003) indicated that *Leonodus* had *Antarctilamna*-type scales and fin spines, based on an associated (but not articulated) assemblage of remains on a single slab from the type locality for *Leonodus*. No teeth from the Cravens Peak Beds localities are comparable with *Leonodus* teeth.

Machaeracanthus pectinatus sp. nov (Figs 6A-C,7A-L,8A-E)

1987 'shark scales comparable with those of *Gualepis*' Turner & Young: 233
1987 '*Machaeracanthus* spines and scales' Young et al.: 239
1991 'shark scales cf. *Gualepis*' Turner: fig. 5G-H, pl. 5I
1991 '*Machaeracanthus*' Turner: tab. 3
1993 'scales similar to those called *Gualepis*' Turner: 184, fig. 8.4G-H
1993 '*Machaeracanthus*' Turner: 193
1993 'machaeraeanthid acanthodians' Young: 224
1995 '*Machaeracanthus* scales' Turner: 683
2000 '*Machaeracanthus* sp.' Young & Turner: 464
2003 'Acanthodian remains', in parts Young & Goujet: 9.

ETYMOLOGY. Latin *pectinis*, comb.

MATERIAL. HOLOTYPE: Scale ANUV2936.10 (Fig. 7A); Locality GY11 (= BMR locality GEO 65/28; Fig. 1B), a small limestone outcrop in the S part of the Toomba Range, W flank of the Toko Syncline, Georgina Basin, western Queensland. **PARATYPES:** Scales ANUV2938.4, ANUV2938.2, ANUV2935.12, ANUV2938.1, ANUV2938.8, ANUV2937.5 (Fig. 7B-G) and thin sections of scales ANUV2939.1-3 (Figs 6A-C,7H,J,K). **ADDITIONAL MATERIAL.** Eighty-one scales including three ground thin sections from samples ANU V2935-41, and ca. 20 scales from ANUV2969, locality GY11; probably four scales including CPC20087/3 from sample 74710577 (locality GEO 65/28); possibly one scale from shot-point sample SP801; possible fin ray-type elements from localities GY10,11 (Fig. 1B).

DIAGNOSIS. Scales with four to twelve sub-parallel or sub-convergent ridges on the anterior part of the crown, and sub-parallel denticulations forming the posterior crown and extending behind the base; individual flank scales have a similar or equivalent number of ridges as denticulations; scale neck and base are of equal height; orthodentine forms most of the crown, with some mesodentine in the anterior part of the crown growth zones; growth zones are apposed in the posterior, and superposed in the anterior region of the crown.

GEOGRAPHICAL AND STRATIGRAPHIC DISTRIBUTION. Cravens Peak Beds (?late
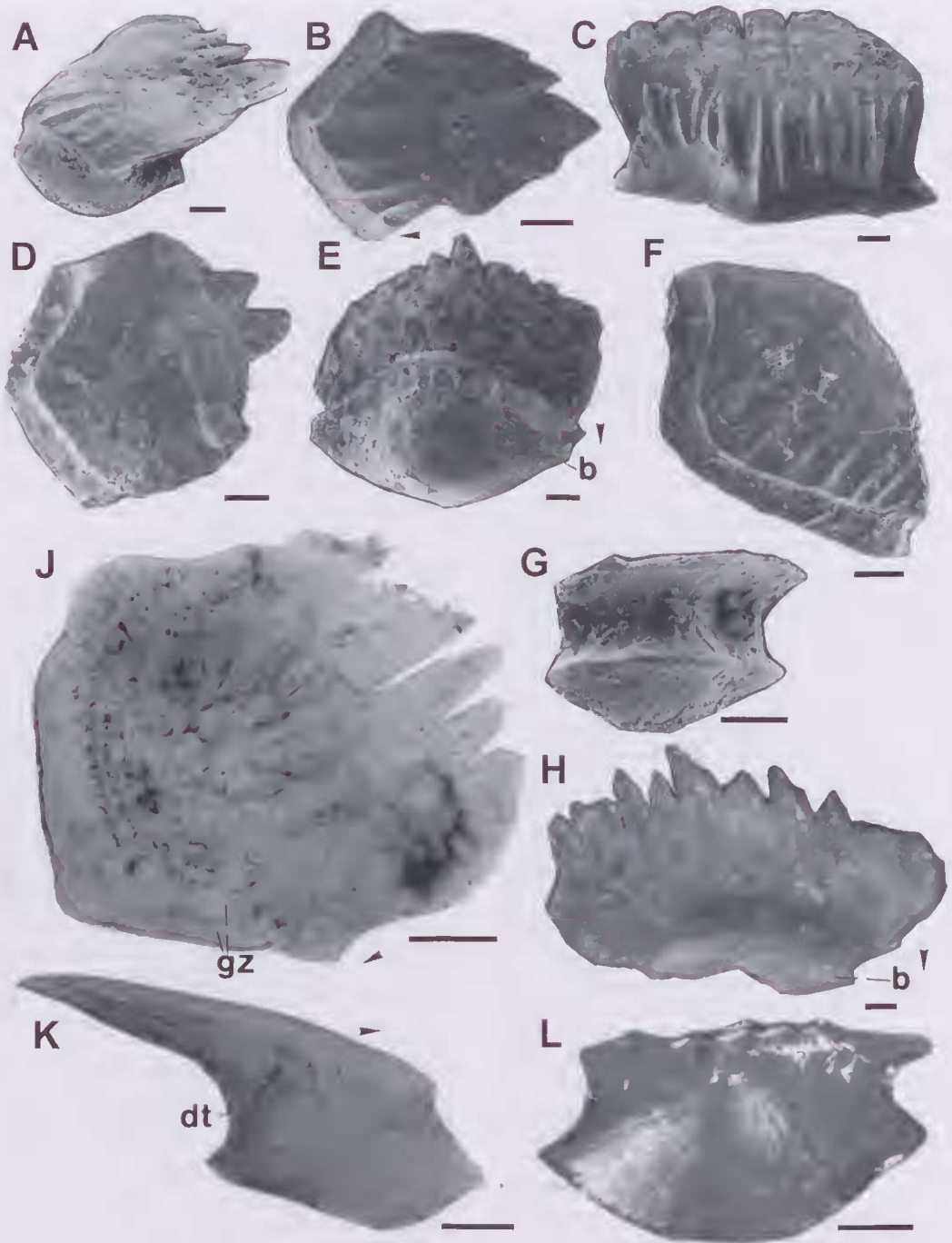
FIG. 7. Scales of *Machaeracanthus pectinatus* sp. nov. from site GY11. A, latero-crown view, ANUV2936.10; B, crown view, ANUV2938.4; C, antero-crown view, ANUV2938.2; D, crown view, ANUV2935.12; E, basal view, ANUV2938.1; F, crown view, ANU V2938.8, posterior crown section broken off; G, posterior view, ANUV2937.5; H, basal view, ANUV1649.1 anterior of scale broken off; J, horizontal section of crown ANUV2939.1; K, vertical longitudinal section ANUV2939.2; L, vertical transverse section ANUV2939.3, under cross nicols. Scale bar = 0.1 mm; arrow to anterior; b = base, dt = dentine tubules, gz = crown growth zones.
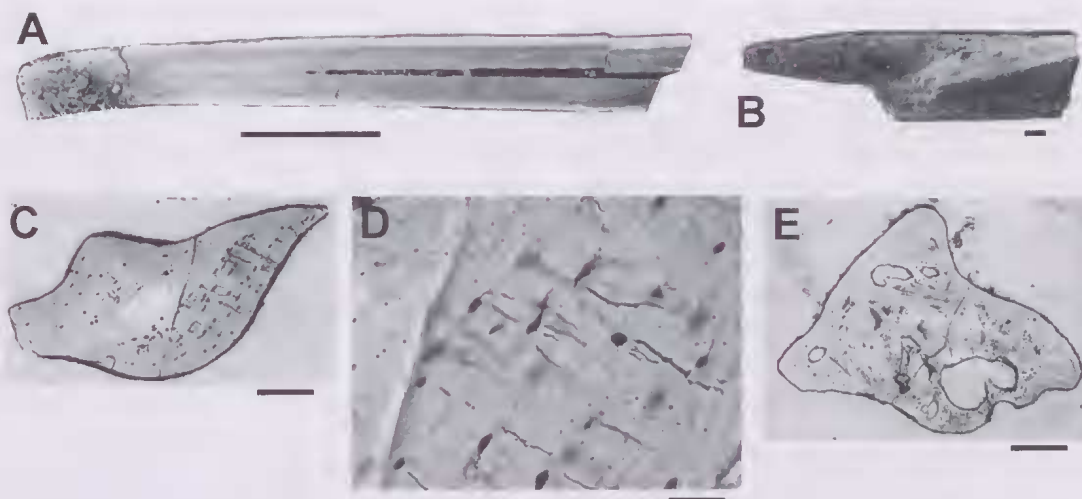
FIG. 8. Fin ray or spine elements possibly from *Machaeracanthus pectinatus* sp. nov. from GY10 (A,B) and GY11 (C-E). A, double element fused at base (left) ANUV2941.1; B, single element with narrow proximal end ANUV2941.2; C-D, transverse section from distal part of an element ANUV2939.18: C, showing whole section, D, close-up of bone cell lacunae and processes; E, transverse section from proximal part of an element ANUV2939.19. Scale bar = 1mm in A, 0.1mm in C,E, and 0.01mm in D; C-E, under cross nicols.

Emsian/early Eifelian), Toomba Range, Georgina Basin, western Queensland

DESCRIPTION. *Morphology* (Fig. 7A-H). Scales translucent, amber or cream coloured, with small red spots throughout the latter type; 0.7 to 1.2mm wide and long. Crown rises slightly or steeply antero-posteriorly, extending well beyond the posterior corner of base on well-preserved scales. Between four and twelve sharp ridges lead back from the anterior edge of the crown; on some scales these ridges tend to converge, while on others they run more or less parallel to each other. The posterior crown, when preserved, is divided into five to eleven long parallel denticulations. The neck is short and concave all round, with a sharp rim between the neck and base. Base shallow to moderately convex with swelling central, or sometimes forward of centre. Base protrudes only slightly in front of the anterior edge of the crown. Base and neck of the scales of equal height.

Histology (Figs 6A-C,7J-L). No bone cell lacunae or wide vascular canals are visible in the base or crown. Orthodentine tubules radiate through most of the crown, extending into the posterior crown 'fingers'; some mesodentine with a network of lacunae and short tubules is developed in the front of the crown. Apposed growth zones form the posterior crown, and superposed zones form the anterior crown.

?Fin spines or rays (Fig. 8A-F). 0.5 to 1mm wide, asymmetrical, slightly tapering along the main shaft. Surface smooth except for irregular longitudinal grooves of the vascular system visible towards proximal end. In cross-section of the distal ends, the 'dorsal' side has a rounded ridge, slightly off-centre, the 'ventral' side is bowl-shaped, and the edges flatten out to be relatively thick and blunt on one side, and thin and pointed on the other side. Elements have a dull, 'bony' lustre. ANUV2941.1 comprises two rays fused at the base (Fig. 8A). Histological structure of distal fragments (Fig. 8C,D) shows no dentine tubules or vascular canals, but abundant bone cell lacunae, some of which have ?Williamson's canals leading towards the exterior. Mid-shaft, the 'dorsal' ridge is very asymmetrical, curving over towards the side. Histological structure at this level (Fig. 8E) shows weak growth lines paralleling the external surface, with some short straight canals in these narrow outer growth zones. The inner part is formed of thick bone, similar to tissue described by Bystrow (1957) in non-dentinous placoderm bones, with abundant bone cell lacunae and wide, longitudinal vascular canals.

REMARKS. Scales are the only certain machaeracanthid elements in the Cravens Peak samples. *Machaeracanthus bohemicus* (Barrande, 1872) from Lochkovian to early Emsian limestones in the Czech Republic is the only *Machacracanthus* with more than one type of element assigned to it: material from the Czech localities includes spines associated with scales, a scapulocoracoid and possibly the tip of a tooth (Zidek, 1985). Isolated scales from Early Devonian localities worldwide have been assigned to *Machacracanthus* sp. (e.g. Goujet, 1976; Mader, 1986; Wang, 1993; Burrow, 1997). Scales from the Lochkovian of northern Spain assigned by Wang (1993) to *M. stonehonsensis* have 'Stranggewebe'-like tissue (i.e. with close-set, parallel elongated lacunae) in the crown, and other *Machaeracanthus* sp. scales from the Early Devonian of Spain (Mader, 1986; Wang, 1993) and France (Goujet, 1976) have bone cell lacunae in the base, and vascular canals and probably mesodentine in the crown. Cravens Peak Beds machacracanthid scales have similar histological structure to *M. bohemicus;* orthodentine forming most of the crown, on-layering or apposition of growth zones in the posterior crown denticulations (e.g. Gross, 1973: pl. 28.21a) and lacking bone cell lacunae. Scales of *M. pectinatus* sp. nov. differ to those of *M. bohemicus* by the comb-like structure formed by the sub-parallel denticulations of the posterior crown (in the latter species, the denticulations radiate from the centre of the scale) and having a shallower scale base.

Except for *Machaeracanthus pectinatus* sp. nov., all other *Machaeracanthus* scales are from Lochkovian strata. *Machaeracanthus* sp. scales from near Trundle, New South Wales are now thought to be from two taxa (Burrow, 2002). Older scales from the Connemarra Formation (= 'Trundle Beds B' in Burrow, 1997; late Lochkovian/ early Pragian) are now considered indeterminate, deriving from either *Machaeracanthus* sp. or the Poracanthodidae, while scales from the younger Troffs Formation (= 'Trundle Beds A' in Burrow, 1997) and Gleninga Formation (mid Pragian-early Emsian) are now assigned to *Chciracanthoides wangi* (Basden et al., 2000; Burrow, 2002; Burrow et al., 2000). Turner (1991, 1993) compared some of Cravens Peak Beds *M. pectinatus* sp. nov. scales to those of the chondrichthyan *Gnalepis*. Several of the scales in the type material of *Gnalepis* Wang, 1984 from the Xitun Member, Cuifengshan Formation, China which were designated 'old' scales (e.g. those in Wang, 1984: figs 10D-E,11A-D) are possibly specialised ischnacanthid scales. Similar scales assigned to *Machacracanthus pectinatus* sp. nov. probably lined sensory canals on the head of the fish. However, *Gnalepis* scales from the type locality in China which were described as juvenile scales appear to be chondrichthyan, not acanthodian.

Zidek (1981) characterised different species of *Machaeracanthus* by the cross-sectional shape of fin spines. Unfortunately, histological study of the spines is limited: no thin sections of *M. bohemicus* spines were located in the Czech National Museum collection. Large *Machacracanthus* sp. spines have been described from the Lower or Middle Devonian of North and South America, Antarctica, Africa, Europe and the Falklands Islands (Maisey, 2002). While it is by no means certain that the fin ray-like elements from the Cravens Peak Beds belong to the same fish as the *M. pectinatus* scales, the elongated elements have a similar cross-sectional shape to spines of *M. major* (Zidek, 1981: fig. 2e). However, lack of an outer dentine layer and occurrence of fused elements in the Cravens Peak Beds elements indicate they are not homologous with normal acanthodian fin spines. Rather, they probably derived from internal fin rays. If so, they suggest an explanation for the difference between fin spines of *Machaeracanthus* and other acanthodians (if *Machaeracanthus* is indeed an acanthodian). Fin spines of acanthodians are typically found in front of all fins except the caudal, and in all other acanthodian genera they have a U-shaped cross section. *Machaeracanthus* has only asymmetrical, presumably paired, spines, in which the pulp cavity is always totally enclosed by the spine body. Perhaps *Machaeracanthus* fin spines are not homologous with those of other acanthodians, but developed from enlarged radials of the pectoral fins. All fins in the mesacanthid acanthodian *Triazengacanthus* (Gagnier, 1996: figs 8,14) have 'ceratotrichia' with a circular cross-section, and some of these elements are forked (P.-Y. Gagnier, pers. comm.), but they are only about 0.02mm wide (compared to their pectoral fin spines which are about 6mm long). Amongst the ischnacanthiforms, *Ischnacanthus gracilis* had 'ceratotrichia' (diameter ca. 0.01mm) in the proximal part of the fin web (Miles, 1970: fig. 8), articulating with basal radials. If machaeracanthids derived from an ischnacanthiform ancestor, perhaps *Machaeracanthus* spines developed by

enlargement of the fin basals after loss of the pectoral fin spines. Although younger than *M. bohemicus*, *M. pectinatus* sp. nov. could represent an intermediate stage in phylogenetic development of *Machaeracanthus*. No dentinous *Machaeracanthus* fin spines have been recorded from Australia or any other region of East Gondwanaland, suggesting the *Machaeracanthus* lineage split before typical, large ?dentinous spines developed elsewhere. Development of spines from internal fin rays in the paired fins has occurred numerous times in different groups including extant fishes such as catfishes, lionfishes and bullheads, and perhaps also the enigmatic chondrichthyan *Menaspis armata* Ewald, 1848 from the Permian of Germany. Work on extant *Channallabes apus* (Adriaens et al., 2002) showed maximum variability in development of pectoral fins and spines, with individuals in one generation having these structures and some individuals in the next generation lacking them. In the light of such studies, the reinvention of a pectoral fin spine in *Machaeracanthus* is not unlikely.

Despite similarity between the Cravens Peak Beds asymmetrical fin rays and fin spines from *Machaeracanthus*, the possibility that they could be from one of the other types of fish in the samples must be considered. Unfortunately, the shape and histology of fin rays from other Mid-Palaeozoic fish have only rarely been described (e.g. Goodrich, 1904). Reconstructions in Stensiö (1959) show pectoral fins in arthrodire placoderms with distally-branching radials. A totally bony structure is the norm for osteichthyan dermal fin rays (as opposed to lepidotrichia, which are specialised scales). The Carboniferous sarcopterygian *Rhizodus* had bifurcating fin rays, but these have a circular cross-section (Andrews, 1985: fig. 4d-f). Some actinopterygians (e.g. *Pachyrhizodus* from the Cretaceous of Queensland) had fin rays with a cross-sectional shape and internal structure similar to the Cravens Peak Beds elements. Fin rays of the dipnoan *Scaumenacia curta* (Goodrich 1904: fig. 33A) and the osteolepiform *Eusthenopteron foordi* (Goodrich, 1904: fig. 45B) have a histological structure which also is comparable with that of the Cravens Peak Beds elements, but the cross-sectional shape of the rays in these sarcopterygian taxa is sub-circular. In conclusion, an assignation of the fin rays to *Machaeracanthus pectinatus* is only tentative.

CONCLUSIONS

Differences in the vertebrate taxa from the SP799 shot-point locality and the other localities indicate different ages. SP799 vertebrate fauna includes scales of thelodont *Turinia* sp., rare scales of *Nostolepis* sp. cf. *N. striata*, and *Radioporacanthodes?* sp. (Burrow, 2002). All three are also found in the ?late Lochkovian/ early Pragian Martins Well Limestone. The acanthodians *Teneracanthus toombaensis* gen. et sp. nov. and *Machaeracanthus pectinatus* sp. nov. are added to the extensive late Early to early Middle Devonian vertebrate faunal list from the Cravens Peak Beds (Young & Goujet, 2003). As all other scale-based species of *Machaeracanthus* are from the Lochkovian or Pragian, *M. pectinatus* sp. nov. is the youngest *Machaeracanthus* species for which scales have been identified. The oldest mesacanthid taxon *Mesacanthus mitchelli* is Early Devonian (Lochkovian), and the youngest mesacanthid taxa are the Late Devonian (Frasnian) *Lodeacanthus gaujicus* and *Triazeugacanthus milesi*. *Teneracanthus toombaensis* gen. et sp. nov. appears intermediate between these taxa, being most closely related to *Lodeacanthus*.

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